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9. McGee (*8*) estimated that the green turtle constituted 25 percent of the Seri diet.
10. A number of astute Mexican and Seri fishermen, well known by us, report that turtles have become increasingly scarce, particularly in the last decade. [Also see O'Donnell (*11*); J. J. Parsons, *The Green Turtle and Man* (Univ. of Florida Press, Gainesville, 1962); R. Marques Millan and A. Villanueva O., *Gac. Coop. No. 52* (1974), p. 30.]
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12. Standard phonemic conventions are used here, as in (*4–6*).
13. Our preliminary data indicate that the green turtle is dormant at water temperatures below approximately 15°C. For example, on 21 January 1974, at the north end of the Infiernillo Channel, turtles were active on the bottom at 18°C, and on 23 January 1975, we found dormant turtles off San Esteban Island at 14°C at a depth of 8 to 10 m. For surface water temperatures in the Gulf of California, see M. K. Robinson, *San Diego Soc. Nat. Hist. Mem. 5* (1973).
14. The Mexican fishermen use open fiberglass boats (*boas*), generally 7 m long with 25- to 40-horsepower Johnson or Evinrude outboard motors. For turtle hunting the Seri prefer their somewhat smaller and more maneuverable plank boats, also with outboard motors.
15. Epizoophytic marine algae are common on winter turtles in the Gulf of California, but not on those taken in summer. J. N. Norris (in preparation) has identified more than 20 species of epizoophytic algae from winter *Chelonia* discussed here. See also G. J. Hollenberg, *J. Ariz. Acad. Sci.*, in press.
16. We have detected little difference between summer and winter catches, although catches of *caguama echada* usually include a higher percentage of large adult animals. For dormant winter turtles, *caguama echada*, in 1975: $N = 69$, range of carapace length = 50.0 to 92.5 cm, mean ± standard deviation (S.D.) = 68.9 ± 9.96 cm. For summer *Chelonia* from same region, 1974 and 1975: $N = 67$, range = 47 to 88 cm, mean ± S.D. = 65.3 ± 10.36 cm. Adult males are in the Gulf of California throughout the year, although females are more numerous; see also (*2, 3*).
17. Although the green turtle has become more scarce in recent years (*10, 11*), exploitation of dormant winter turtles produces particularly rapid results. In January 1975 hunting was intensified around San Esteban Island. Depletion of these turtles stimulated rapid expansion of winter hunting throughout the midriff islands and to Baja California (Fig. 1). The efficiency of the new methods is indicated by the great enthusiasm of the fishermen for them and by the rapidity with which one area is depleted and the hunters move on. We have been able to gather some relevant numerical data. In late May 1975 four parties that "summer-hunted" [see Caldwell (*3*) and O'Donnell (*11*)] for 23, 20, 25, and 12 hours of real effort each obtained $N =$ 13 (total weight = 247 kg), 13 (413 kg), 13 (384 kg), and 6 (?kg) turtles, respectively. In January 1975 two parties that "winter-hunted" for 7 to 8 hours of real effort each obtained $N = 26$ (> 800 kg) and $N = ?$ (718 kg) turtles, respectively. These rates of success provide high economic incentives.
18. Some aquatic reptiles may extract some oxygen directly from the water [D. Jackson and K. Schmidt-Nielsen, *J. Cell. Physiol.* **67**, 225 (1966); D. Belkin, *Respir. Physiol.* **4**, 1 (1968); J. Graham, *ibid.* **21**, 1 (1974)]. If buried turtles cannot use this strategy their anaerobic capacity may be great, although one study in Florida suggested a surprisingly small anaerobic capacity for sea turtles in contrast to other turtles [D. Belkin, *Science* **139**, 492 (1963)].
19. Nesting beaches and reproductive migrations of these populations are not known. The fishermen believe that the nesting beaches are in Sinaloa, Mexico.
20. We thank the Seri for sharing their knowledge. We thank the fishermen at Kino Bay for extended cooperation and express deep concern for their economic welfare, which depends on diminishing marine resources. For assistance in the field we thank M. Drees, G. Kooyman, J. N. Norris, M. Owens, A. Russell, J. Russell, A. Topete, and J. Turner. B. L. Fontana and J. R. Hendrickson provided valuable discussion, and the staff of the Centro Regional del Noroeste of the Instituto Nacional de Antropología e Historia helped in many ways. Supported by NSF grant SOC 75-13-628 to R.S.F. and a University of Minnesota graduate school grant to P.J.R.

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Island Biogeography Theory and Conservation Practice

Abstract. *The application of island biogeography theory to conservation practice is premature. Theoretically and empirically, a major conclusion of such applications—that refuges should always consist of the largest possible single area—can be incorrect under a variety of biologically feasible conditions. The cost and irreversibility of large-scale conservation programs demand a prudent approach to the application of an insufficiently validated theory.*

Recent interest has been generated in the application of island biogeographic theory to the design of wildlife refuges, especially through a news brief by May (*1*), who has summarized recent studies on birds (*2, 3*) as a basis for specific conservation suggestions of general utility, while cautioning that current models do not incorporate potentially important biological facts. We propose that the proof of the underlying theory has not been so broad that conservation applications ought clearly to follow, and that the main specific suggestion (*4*)—that refuges should always consist of the largest possible single area—need not be correct. Hooper's suggestions along the same lines (*5*) seem not to have been heeded. It is important to enlarge on Hooper's views and to present new evidence because widely publicized briefs may be adopted as canon in conservation planning without appropriate discussion.

The equilibrium theory of island biogeography applies in part to any system, since turnover (extinction and immigration) must occur, given sufficient time (*6*). At issue is the definition of sufficient time; one can reasonably claim for some taxon and location that turnover is so slow that equilibrium will never be reached (*7*). In particular, data implying high avian extinction rates (*8*) have been impugned (*9*). It is these high extinction rates, which are higher on smaller islands because smaller populations are more susceptible to aleatory breeding failure and mortality, that lead to the imperative that refuges be as large as possible (*1*): "In cases where one large area is infeasible, it must be realised that several smaller areas, adding up to the same total area as the single large area, are not biogeographically equivalent to it: they will tend to support a smaller species total."

The same species-area relationship cited by advocates of single large preserves could as well be adduced in support of several small ones. If $S = kA^z$ (where S is the number of species; A is the area; and k and z are constants, the latter in the vicinity of 0.2 to 0.35 for most taxa and regions), let us consider the following decision. We may construct either one large refuge of area A_1 or two small ones each of area $A_2 = A_1/2$. By which plan would we preserve the most species? Each of the two small refuges would have $S_2 = kA_2{}^z$ species. If all species P in the species pool are equally adept at dispersing to and surviving in refuges, the expected total number of species in the two refuges together (species in both refuges counted once) would be $2S_2 - S_2{}^2/P$ (*10*). More realistically, we would hypothesize a gradient of total species number between S_2, where a well-defined gradient of dispersal and survival abilities exists, and $2S_2$, where no such gradient exists but where competitive interactions prevent many pairs of species from coexisting in the same refuge (*11*). In contrast, how many species, S_1, might we expect in one large refuge of area A_1? Letting $z = 0.263$ (a widely used value for log-normal distributed population sizes; the qualitative result does not depend on the exact value of z),

Table 1. Relative numbers of species in one large refuge (S_1) as compared to the number of small ones containing S_2 species each. The P species in the regional pool are assumed to be noninteracting and equally adapted to refuge existence.

N	S_T = total species in N refuges	Factor by which S_1 exceeds S_2	Minimum fraction S_l/P for which $S_T > S_1$
2	$2S_2 - (S_2{}^2/P)$	1.200	0.960
3	$3S_2 - 3(S_2{}^2/P) + (S_2{}^3/P^2)$	1.335	0.981
4	$4S_2 - 6(S_2{}^2/P) + 4(S_2{}^3/P^2) - (S_2{}^4/P^3)$	1.440	0.991
5	$5S_2 - 10(S_2{}^2/P) + 10(S_2{}^3/P^2) -$ $5(S_2{}^4/P^3) + (S_2{}^5/P^4)$	1.527	0.995

we find that $S_1 = kA_1{}^z = k(2A_2)^z = 1.200 \times S_2$. This is less than the expected number in the two small refuges for $S_1/P < 0.960$; surely a refuge designed to maintain 96 percent of all species in a region would be considered ambitious. Furthermore, the more (and smaller) refuges posited as an alternative to a single large one, the more likely is the archipelago of small refuges to contain more species (Table 1). If anything, competition should exacerbate this disparity.

One of us (D.S.S.) has performed an experiment which tests this hypothesis. During autumn 1971, in five small red mangrove (*Rhizophora mangle*) islands, a census was taken to determine their arboreal arthropod communities; the islands and census methods have been described (*12*). In December 1971, the experimental islands were each turned into a small archipelago by excavation of permanent, water-filled channels through the bases of the islands and by removal of the canopy above the channels. The width of the channels between vegetation on either side is at least a meter. In April 1975 a census of two of these archipelagoes, consisting of four and two islands, respectively, was taken. Earlier experiments (*13, 14*) suggest that a distance of 1 to 2 meters is a barrier to many mangrove colonists and that 3 years is sufficient for equilibration. The results from archipelago A (Table 2) support the contention that a cluster of small refuges might be expected to have more species than a single large one, although a single experiment cannot be viewed as strong evidence.

One need not invoke competition to explain this result; a group of investigators, whose reports have been reviewed by Levin (*15*) stress the theme of continued extinction and reinvasion in a patchy environment. Possibly the increased extinction rates on the individual islands in this mangrove archipelago are more than compensated for by the presence of the other islands as nearby sources generating high propagule (reproductive units) invasion rates. One can also conceive of environmental catastrophes (such as certain kinds of forest fires or contagious diseases) that could cause extinction if all conserved lands were united in one large refuge but would be inconsequential in one of a network of small refuges.

If we stopped here we would be guilty of oversimplification. There is a limit beyond which subdivision produces refuges and, therefore, population sizes so small that extinction rates are greatly increased. The results from mangrove archipelago B (Table 2), consisting of smaller islands, may exemplify this principle. On demographic grounds one may predict that the increase in extinction rates with decrease in population size will be particularly rapid below some "critical population size" (*10, 16*). Critical population sizes must differ between species, as must the area necessary to support a large enough population to be relatively immune to fast extinction. An experiment on mangrove islands (*17*) confirms increasing extinction rates throughout an island for smaller islands; however, Heatwole (*18*) provides evidence for a characteristic "minimum insular area" for each of several reptilian taxa. Similarly the observation (*19*) that different bird families have different species-area curves and a review (*20*) of evidence for higher species-extinction rates for predators would support the idea that all species are not ecologically equal. This would have a clear corollary that not all species require the same conservation regime. Furthermore, since populations exist as components of larger entities, for certain species it may not be realistic to consider conservation of a species rather than a community (*21*).

Table 2. Numbers of arboreal arthropod species on two mangrove islands turned into archipelagoes.

Island	Area (m^2)	No. of species
Original A	475	77
A1	119	51
A2	133	48
A3	80	47
A4	102	50
Archipelago A	434	81
Original B	168	56
B1	71	36
B2	87	32
Archipelago B	158	47

At the other end of the spectrum of refuge sizes, one might predict that, if even small refuges have virtually all the species in the pool, then having several small refuges is not likely to increase the total number of species. Abele and Patton have examined the arthropods of many neotropical coral heads and noted that, when two small coral heads are compared to one large one of equal total area, the pairs consistently contain more species (*22*). But two large coral heads have no more species than a single larger one of equal area. The critical value of $S_1/P \simeq 0.175$ separates the two cases for this biota. So in addition to a consideration of which species we aim to conserve, we must consider what fraction of the pool they comprise. Certainly for "fugitive" species adding up to a small fraction of a regional biota a single large refuge could be exactly the wrong strategy. Matters of cost may also be important (*5*); lower per-unit-area cost of larger patches of land may add to the advantages of size and continuity. It may be possible to strike a balance between the two opposing strategies by constructing corridors among a network of small refuges (*23*).

This is not a plea, then, for a specific conservation regime, but rather for more comprehensive autecological consideration. Terborgh concludes that tropical forest birds rarely disperse over even small unforested distances and therefore require large refuges, while the severe reduction of eastern U.S. forest has caused the extinction of at most two bird species from the Nearctic avifauna (*3*). Similarly, populations of some host-specific phytophagous insects are reduced by habitat fragmentation (*24*), but Elton's suggestion that enormous rain forest reserves are needed for protection of many tropical invertebrates (*25*) may be too pessimistic in view of the well-studied dispersal capabilities even of flightless forest arthropods (*13*). In sum, the broad generalizations that have been reported are based on limited and insufficiently validated theory and on field studies of taxa which may be idiosyncratic.

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